

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 2229

SEPTEMBER 10, 1965

Specific Limits of the Yucatan Flycatcher, *Myiarchus yucatanensis*

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Three members of the flycatcher genus *Myiarchus* breed throughout the Yucatán Peninsula of México. Two of these, *M. tuberculifer* and *M. tyrannulus*, have other populations distributed from the southwestern United States to northern Argentina. The third, *M. yucatanensis*, is endemic and has the distinction of having the most restricted distribution of any mainland species of this genus north of Colombia. J. A. Allen's suspicions (1892) of the specific distinctness of *yucatanensis* were based largely on the very worn condition of the two original specimens, including the type in the American Museum of Natural History which was described by Lawrence in 1871. Allen had difficulty in separating this form from *M. tuberculifer*, as did Salvin and Godman (1889). The peculiar restriction of *yucatanensis* to the Yucatán Peninsula and its geographical and morphological proximity to the *stolidus* group in the Greater Antilles led to speculation as to its affinities with that polymorphic assemblage of insular populations of *Myiarchus* (Ridgway, 1887; Sclater, 1888; Nelson, 1904; Hellmayr, 1927). More recently, Bond (1956) has suggested that *yucatanensis* and *stolidus* may be conspecific, but Paynter (1955) expressed doubt that these two forms are necessarily more closely related to each other than to other members of the genus. Zimmer (unpublished notes) likewise doubted a close affinity of *yucatanensis* with the Greater Antillean

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forms, but felt that certain characters placed it near *tyrannulus*. In a note dated March 20, 1953, Zimmer wrote of *yucatanensis*: "In view of uncertainty, best kept as a species." These conflicting opinions regarding the relationships of the Yucatán Flycatcher to its congeners prompted the investigation reported here.

Field experience with *yucatanensis* was obtained on two trips to Yucatán, from May 25 to June 1, 1959, and from April 22 to 27, 1963. During both visits, activity was concentrated in the vicinity of Chichén-Itzá where three *Myiarchus* species are sympatric. Observations were made of the behavior and interaction of all three species, sound recordings were obtained, and specimens were collected. During visits to a number of the Greater Antillean islands in April, 1960, and April, 1963, I became familiar with the *M. stolidus* group and obtained sound recordings and specimens for comparison. An analysis of the interrelationships of the insular populations of *M. stolidus* will be published separately. Recording equipment in 1959 and 1960 consisted of a Magnemite recorder operated at 15 inches per second, a preamplifier, and an Altec 660B microphone mounted in a 24-inch parabolic reflector. In 1963 the field recorder used was a Uher 4000 Report operated at 7.5 inches per second. Representative vocal patterns were then selected for analysis with a sound spectrograph. The spectrograms presented here were chosen to demonstrate the extremes of variation evident from this analysis. Museum specimens were examined and analyzed for morphological variation. Lack of adequate material in juvenal plumage has necessitated restriction of this definition of specific limits to adults (non-juvenal plumaged). Linear measurements, in millimeters, were taken as follows: wing, flattened; tail, from the insertion of the central rectrices; bill length, from the anterior margin of the nostril; bill width and bill depth, at the anterior margin of the nostril. In the diagramming of statistical analyses, 1.3 times the standard deviation was plotted on each side of the mean (forming a solid rectangle). Thus, when two samples are compared, non-overlap of the solid rectangles indicates the probability that at least 90 per cent of the individuals of one population are separable from 90 per cent of the individuals of the other population with respect to the particular character that is analyzed.

This study was supported by grants from the National Science Foundation (G-7083) and the Frank M. Chapman Memorial Fund (1963). I am indebted to Colonel and Mrs. D. S. McChesney of Syracuse, New York, for contributing to the success of the field work in 1959. For the loan of specimens and permission to examine collections I am grateful to the curators of the following museums: Carnegie Museum (C.M.): Chi-

cago Natural History Museum (C.N.H.M.); Museum of Comparative Zoölogy, Harvard University (M.C.Z.); Museum of Zoology, Louisiana State University (M.Z.L.S.); Museum of Zoology, University of Michigan (M.Z.U.M.); Peabody Museum, Yale University (Y.U.); and the United States National Museum of the Smithsonian Institution (U.S.N.M.).

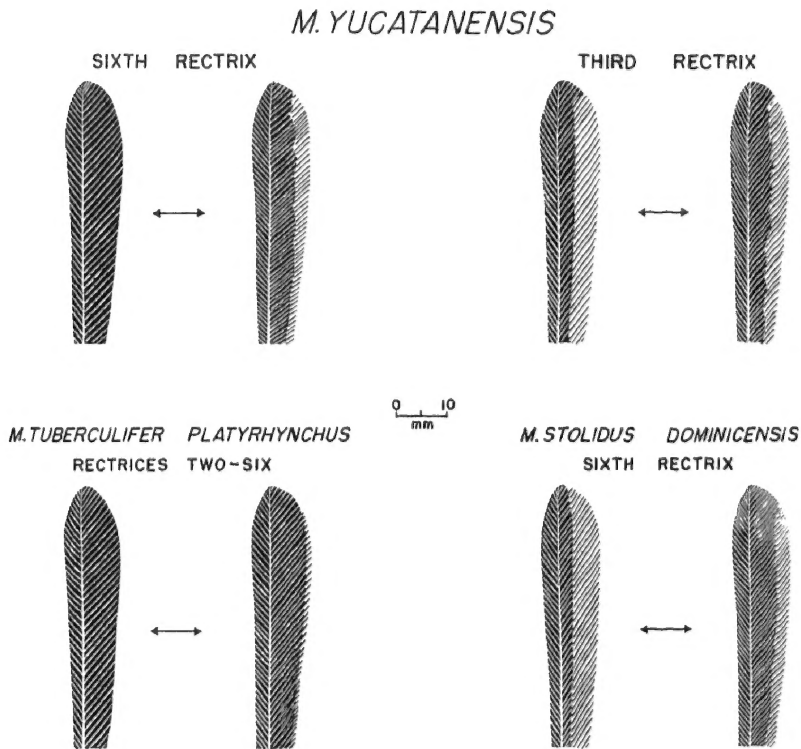


FIG. 1. Limits of individual variation in extent of rufous coloration in the tail, represented by lighter area on larger, inner vane of each rectrix. Rectrices are numbered from the center. Sample sizes: *Myiarchus yucatanensis* (51), *M. tuberculifer platyrhynchus* (58), and *M. stolidus dominicensis* (65).

Throughout its restricted range, *yucatanensis* is in close association with *M. tuberculifer platyrhynchus* and *M. tyrannulus cooperi* and exhibits no evidence of hybridization with these congeners. In the field it is easily separable from *cooperi* on the basis of its conspicuously smaller size and distinctive voice (see Lanyon, 1960). In fresh specimens, the orange mouth lining of *yucatanensis* contrasts sharply with the pale ochraceous-buff or "flesh-colored" lining of *cooperi*.

The best single morphological character for separating adult specimens of *yucatanensis* and *platyrhynchus* in the hand is the extent of rufous in the tail (fig. 1). Typical specimens of *platyrhynchus* lack rufous in the inner webs of all rectrices, or they may exhibit a very narrow rufous border (less than 1 mm. wide) to the inner webs of rectrices 2 through 6. In regions where *platyrhynchus* intergrades with *M. t. lawrencei*, in and near the Isthmus of Tehuantepec, and with *M. t. connectens*, in northern British

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF *Myiarchus yucatanensis*

	Sample	Range	Mean, S.E.	S.D.	C.V.
Wing length					
Males	32	81-88	84.9±0.28	1.60	1.88
Females	17	76-82	79.3±0.46	1.89	2.38
Tail length					
Males	29	77-85	81.5±0.42	2.26	2.77
Females	18	70-81	75.8±0.60	2.55	3.36
Bill length					
Males	31	12.1-14.2	13.07±0.09	0.50	3.85
Females	16	11.6-13.1	12.37±0.10	0.42	3.38
Bill width					
Males	33	6.8-7.7	7.28±0.05	0.27	3.65
Females	18	6.4-7.4	6.98±0.06	0.24	3.48
Bill depth					
Males	28	4.9-5.8	5.39±0.04	0.23	4.19
Females	15	4.8-5.7	5.31±0.06	0.23	4.33
Bill length minus bill width					
Males	32	4.5-6.9	5.76±0.09	0.54	9.32
Females	16	4.9-6.0	5.42±0.09	0.34	6.29

Honduras and Guatemala, the rufous border of rectrices 2 through 6 may be as wide as 2 mm. By contrast, the rufous pattern in the tail of *yucatanensis* is well developed. Though the outer rectrix (sixth) may lack rufous in many specimens, the width of the rufous border of the inner web of the third rectrix exceeded 3 mm. in all 51 specimens of *yucatanensis* examined.

Mensural characters for *yucatanensis* are analyzed statistically in table 1. Depth of bill and length of tail are helpful in distinguishing between *yucatanensis* and *platyrhynchus* at the populational level. Analysis of the sample at hand suggests that 90 per cent of the population of *yucatanensis* can be separated from all individuals of *platyrhynchus* on the basis of either

of these measurements, provided the sex of the specimens is known (fig 2). The color of the mouth lining in fresh specimens of both of these forms is orange. I have examined the specimen (Y.U. No. 8718) from Chetumal, Quintano Roo, that Paynter (1955) reported as a possible hybrid between *yucatanensis* and *platyrhynchus*, and I regard it to be well within the range of variation of *platyrhynchus*.

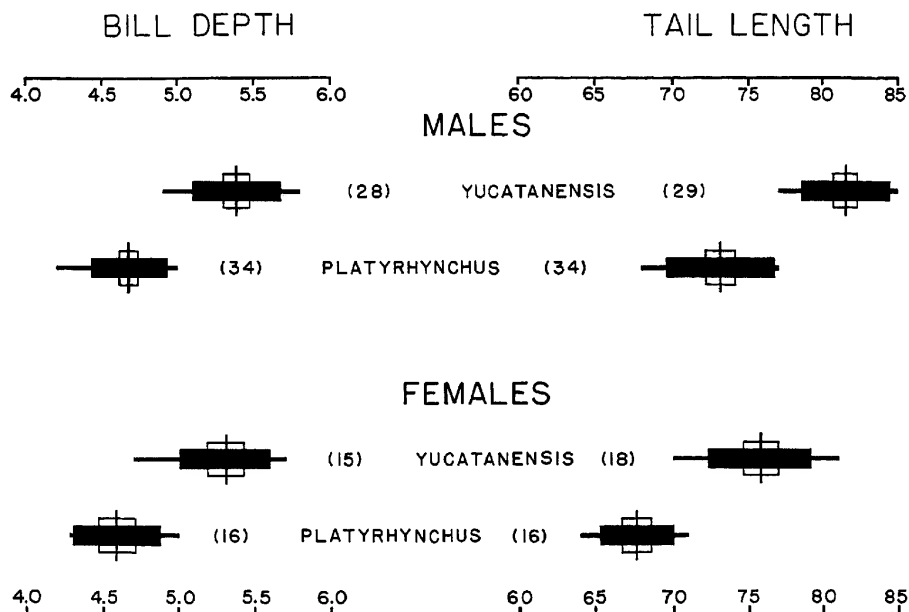


FIG. 2. Population-range diagram of the most diagnostic mensural characters, measured in millimeters, for distinguishing specimens of *Myiarchus yucatanensis* and *M. tuberculifer platyrhynchus*. Sample size in parentheses. Horizontal lines represent range; means are indicated by vertical lines; open rectangles indicate twice the standard error of the mean; solid rectangles indicate 1.3 times the standard deviation.

Separation of *yucatanensis* from the similar-sized *platyrhynchus* in the field can be achieved reliably only on the basis of voice (figs. 3 and 4). Both forms are "whistlers" in that their most characteristic and distinctive vocal patterns are sustained, plaintive whistles of nearly pure tone at about 2.0 kilocycles. The whistle of *platyrhynchus* is typically 0.5 second in duration and nearly always has a symmetrical ascending and then descending pattern. By contrast, that of *yucatanensis* is typically nearer 1.0 second and occasionally up to 1.5 seconds in length. Its most distinctive feature when heard in the field is the very gradual rise in frequency. Occasionally the terminal flourish depicted in figure 3A, not especially

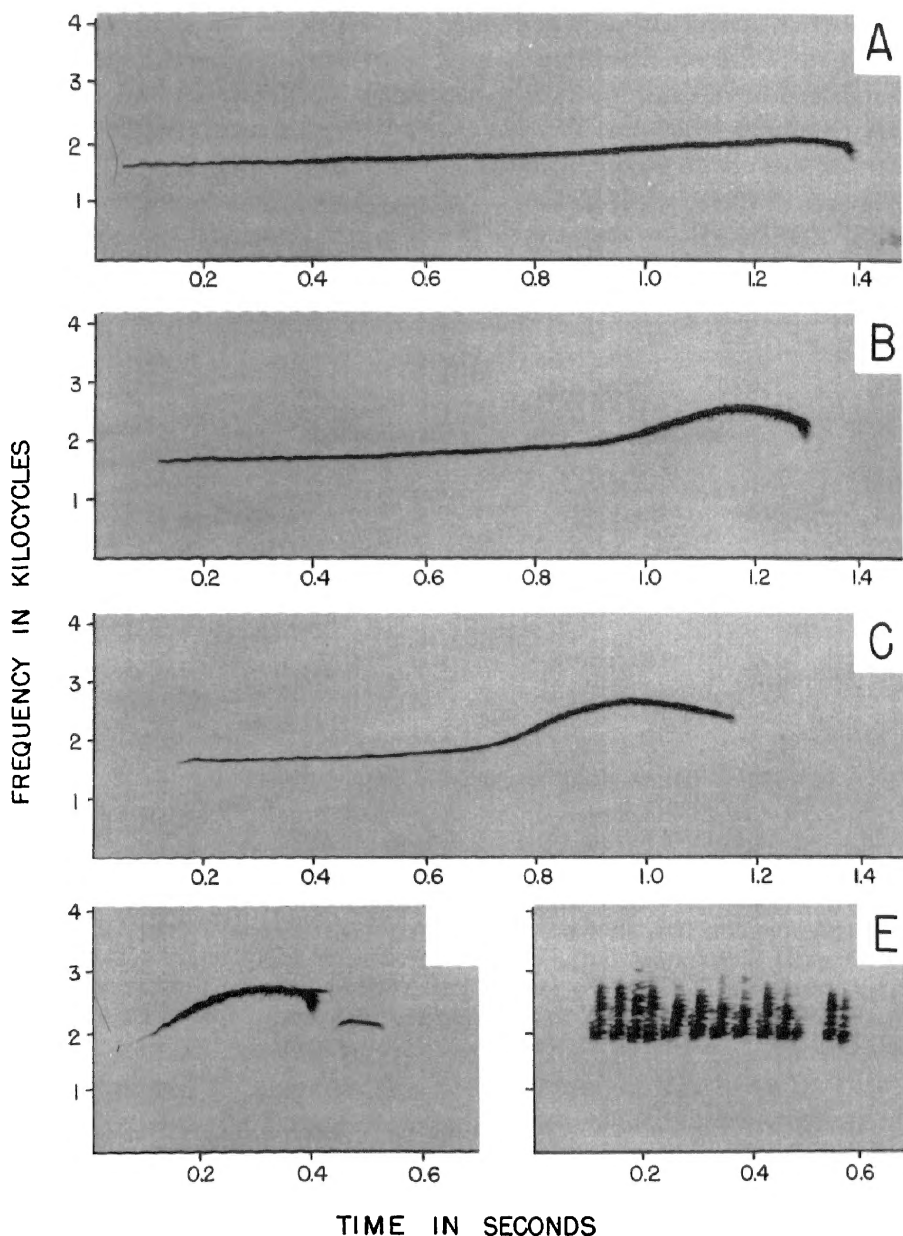


FIG. 3. Sound spectrograms of vocalizations of *Myiarchus yucatanensis*, recorded at Chichén Itzá, Yucatán, on April 26, 1963. A, B, and C. Variations of the most diagnostic vocal pattern of this species, a sustained whistle that gradually rises in frequency. D. The common component of the "dawn song," sometimes alternated with patterns similar to C. Conversational notes, including E, are not unlike the vocal patterns of other members of the genus.

noticeable to the human ear, is exaggerated in the pattern shown in figure 3C, which lends still another distinctive feature not found in the vocal repertoire of *platyrhynchus*. These distinctly different whistled notes also form the basis for the so-called "dawn songs" of these two flycatchers, which are equally useful and conclusive for specific identification.

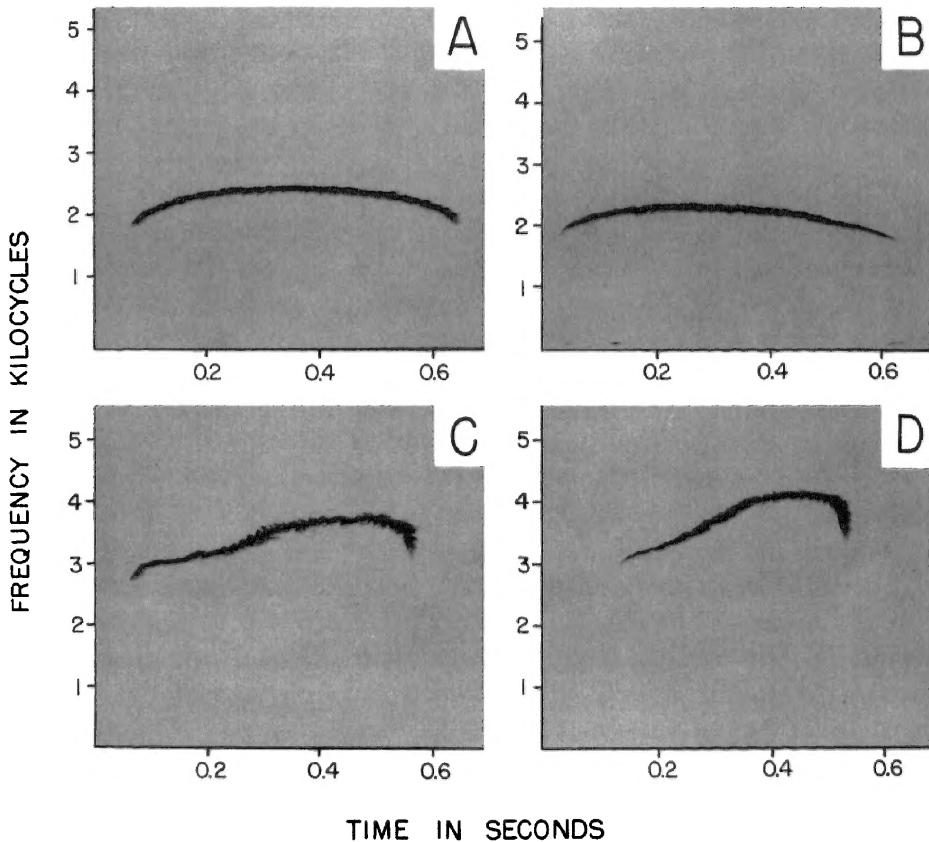


FIG. 4. Sound spectrograms of the most diagnostic vocalizations of two congeners of *M. yucatanensis*. A, B. Vocalizations of *M. tuberculifer*, from recordings made at Barranca, Costa Rica (April 8, 1959), and at Chichén Itzá, Yucatán (April 25, 1963), respectively. C, D. Vocalizations of *M. stolidus*, from recordings made at Good Hope, Trelawny Parish, Jamaica (April 14, 1963).

Morphological characters clearly distinguish specimens of *yucatanensis* from the geographically disjunct and polytypic *stolidus* group, but it is difficult if not impossible to assess the biological significance of such differences among allopatric populations of *Myiarchus*. The Yucatán population is separable at once from all but *M. s. stolidus* (Jamaica) and *M. s. dominicensis* (Hispaniola) on the basis of its straw-yellow abdomen, in

contrast to the white abdomen of the remaining populations. Though *stolidus* and *yucatanensis* have identical rectrix patterns (fig. 1), specimens of these two forms can be differentiated by the darker throat and chest, more extensive rufous on the outer edges of the primaries, browner crown, and greener back in *yucatanensis*. From *dominicensis*, its closest morphological counterpart in the West Indies, *yucatanensis* differs in having a greener back, browner crown, and less rufous in the tail (fig. 1). The most useful mensural character for separating *yucatanensis* from these two Greater Antillean populations is its shorter, wider bill (fig. 5). As in *yucatanensis*, the color of the mouth lining of *stolidus* is orange. I have not seen fresh specimens of *dominicensis*.

There are pronounced differences in vocal characters between *yucatanensis* and the *stolidus* group. The most characteristic vocal pattern of *yucatanensis* has already been described as a sustained, plaintive whistle. The counterpart of this note in the repertoire of *stolidus* on Jamaica is a whistle that is considerably shorter (usually less than 0.5 second) and at a higher frequency (3 to 4 kilocycles). These differences in length and frequency, illustrated in figures 3 and 4, can be appreciated readily by the human ear. A more detailed analysis of the vocalizations of other insular populations of *M. stolidus* is in preparation and will be presented elsewhere.

It has been demonstrated experimentally that differences in vocal characters function as the basis for species discrimination in several members of this genus (Lanyon, 1963). When presented with a variety of vocal repertoires, through the medium of playback of sound recordings, territorial birds react positively only to that repertoire representative of their own species. In the present study, six territorial pairs of *yucatanensis* near Chichén-Itzá were exposed experimentally to sound recordings of *yucatanensis*, *tuberculifer*, *stolidus*, and other congeners, in various sequences. In all these experiments, positive responses were evoked only by the vocalizations of *yucatanensis*. On occasions when a *tuberculifer* recording was utilized, territorial members of that sympatric species responded to the speaker, but not when a recording of *yucatanensis* was played. Similarly, when *yucatanensis* recordings were broadcast for territorial *stolidus* in Jamaica, there was no response. Yet pairs of *stolidus* were stimulated by recordings of their own vocalizations before and after such experiments. I regard this ability to discriminate between characteristic vocal patterns of their respective populations as the most meaningful evidence available for the specific distinctness of *yucatanensis* and the allopatric *stolidus* group.

Though the specific limits of *yucatanensis* are now clear, the affinities of this endemic Yucatán population within the genus *Myiarchus* are far

more difficult to ascertain. Plumage coloration is too variable at the infra-specific level to provide any significant clues to intrageneric relationships, as evidenced by the strikingly divergent rectrix patterns that have been evolved in races of *M. nuttingi* (Lanyon, 1961) and of the variations in upper-part coloration in the many races of *M. tuberculifer*. Mensural characters likewise are of little value, though the only attempt at the sub-

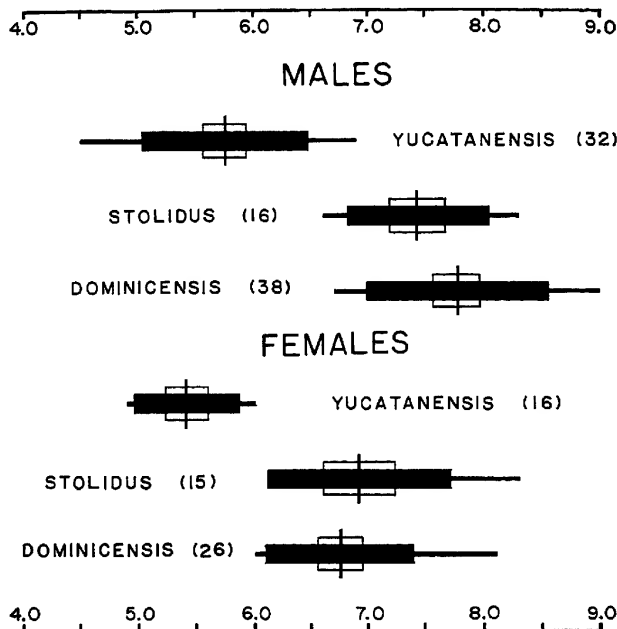


FIG. 5. Population-range diagram of bill length minus bill width, measured in millimeters, for identifying specimens of *Myiarchus yucatanensis*, *M. s. stolidus*, and *M. s. dominicensis*. Sample size in parentheses. Horizontal lines represent range; means are indicated by vertical lines; open rectangles indicate twice the standard error of the mean; solid rectangles indicate 1.3 times the standard deviation.

generic arrangement of *Myiarchus* flycatchers has been based on bill shape. Ridgway (1885, 1893, 1907) and Nelson (1904) separated *M. tuberculifer* and its many representative populations from the rest of the genus on the basis of its comparatively flattened bill (subgenus *Onychopteris* Reichenbach). In the original description (Lawrence, 1871), *yucatanensis* was separated from the *tuberculifer* group on the basis of the fact that the bill was "not so depressed," and the measurements of my series support this view (fig. 2). But if a depressed bill demonstrates a lack of close relationship between *yucatanensis* and *tuberculifer*, then an equally strong argument for lack of affinity between *yucatanensis* and the *stolidus*

group could be based on the fact that the Yucatán population has a bill that is comparatively broad for its length (fig. 5), as noted by Zimmer (unpublished notes) and Paynter (1955).

Diagnostic vocal patterns have been helpful in the definition of specific limits in *Myiarchus*, but it would be presumptuous to attempt an infrageneric classification based on these vocalizations until we have more complete data on the little-known South American forms and until we have some concept of the evolutionary stability of these audio-characters. Hopefully, some insight into the latter may result from my analysis of variation of both morphological and audio-characters among the West Indian populations of *Myiarchus*, now in progress.

The range of *M. yucatanensis* was given by Paynter (1955) as the Mexican states of Yucatán, Quintano Roo, and Campeche. The only record of the species for Cozumel Island, of which Paynter was aware, were the two specimens taken by Gaumer (Salvin and Godman, 1889). I was able to confirm the identification of these specimens as *yucatanensis*, through the kindness of Dr. Kenneth C. Parkes who had them on loan from the British Museum. But, because of the uncertainty of some of Gaumer's localities, Paynter was hesitant in including Cozumel within the range of the species. Griscom, however, had collected a female *Myiarchus* on Cozumel Island on February 25, 1926 (A.M.N.H. No. 254616), but he had not identified it specifically or included it in his published account of the expedition (1926). Zimmer subsequently identified it (on the label) as *tuberculifer platyrhynchus*. I have re-examined the specimen and find it to be *yucatanensis*. More recently, Dr. Robert W. Dickerman collected a female (R.W.D. No. 12536) at Cedral, Cozumel Island, on January 22, 1965, which I have examined and find to be *yucatanensis* and hence it is the second Cozumel specimen extant, in addition to the two Gaumer specimens.

That the range extends southwestward as far as the extreme eastern section of Tabasco has recently been established by D. G. Berrett, whose specimen (M.Z.L.S. No. 24011), taken near Balancán on May 6, 1961, is the first for that state. Two unsexed juveniles and one skeleton, taken at Tikal in the Petén section of Guatemala, in June and July, 1959, have been identified as *yucatanensis* by Paynter (Smithe and Paynter, 1963). I have examined the juveniles (M.C.Z. Nos. 261000 and 261001), but, since we have essentially no data on the specific limits of juvenal-plumaged birds in this group, I cannot determine with certainty whether they are *yucatanensis* or *tuberculifer*. Subsequently Smithe collected two additional specimens from the same locality, and these were males in definitive, basic plumage. I have examined both of these (Smithe's nos. 1312 and 1416), taken at Tikal on September 18 and October 3, 1962, and find them to be *yucatan-*

ensis. Whether or not the species breeds in the Petén is still uncertain. There are no specimens from British Honduras (Russell, 1964), but Edwin Willis has identified *yucatanensis* at Gallon Jug, British Honduras, on the basis of its diagnostic vocal patterns, which he noted from March to July, 1957 (personal communication). Gallon Jug is 130 kilometers southwest of Chetumal, Quintano Roo, where a December specimen has been taken (Paynter, 1955), and only 65 kilometers northeast of Tikal, where Smithe's fall specimens were taken.

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